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Biomechanical Behaviour of Modern Human Molars: Implications for Interpreting the Fossil Record

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ABSTRACT Finite-element models of 29 intact molars were created and subjected to cleavage-type loads in order to assess differences in the biomechanical behaviour of molars. A simulated food particle, which was one-third the size of the intercuspal distance and had the properties of a *Mezzettia* seed, was pushed onto the occlusal basin of these models at various angles, resulting in either both or one particular cusp being preferentially loaded. In all cases, the maximum tensile stresses occurred in enamel at the intercuspal fissure. With regard to first maxillary molars, supporting (functional) and guiding (nonfunctional) cusps apparently dissipate loads equally well, whereas, in second and third maxillary molars, the guiding cusps are better designed to resist loads. Overall, lingual cusps of maxillary posterior molars dissipate loads poorly. Conversely, loads exerted toward supporting cusps of mandibular molars are consistently well dissipated, regardless of position along the tooth row. Because the directions of loads to which these teeth are best adapted change along the tooth row, it seems reasonable to suggest that these may correlate with the well-documented structural and functional orofacial complex. This study indicates that the biomechanical behaviour of molars and the orofacial skeleton are likely to have undergone complementary directional changes during evolution. Consequently, caution must be exercised in making inferences about dietary adaptations of extinct species on the basis of isolated teeth or fragmentary gnathic remains without proper regard of the orofacial skeleton as a whole. Am J Phys Anthropol 106:467–482, 1998.

In all primates, trituration of food follows a similar pattern whereby two phases can be distinguished: puncture-crushing and chewing (Mills, 1955; Crompton and Hiiemäe, 1969; Hiiemäe and Kay, 1972). Whereas the former is achieved through vertical movements of the mandible, chewing involves more medially directed movements. Both the puncture-crushing and chewing cycle, however, are characterised by three comparable stages: the closing, power, and opening strokes (Hiiemäe and Kay, 1972; Griffin and Malor, 1974; Hiiemäe, 1978). During the closing stroke, upper and lower molars are brought toward centric occlusion, such that lingual cusps of maxillary molars intercuspate with the occlusal part of mandibular molars, whereas buccal cusps of mandibular molars intercuspate with the occlusal part of maxillary molars (Hiiemäe and Kay, 1972; Mills, 1955). These cusps have also been referred to as supporting or functional cusps, whereas mandibular lingual and maxillary

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buccal cusps are called guiding or nonfunctional cusps (see, e.g., Kraus et al., 1969) and take part predominantly in the opening stroke of chewing (Kay and Hiiemäe, 1974).

Evidently, teeth are essential for the mechanical breakdown of food, at least in mammals, and their functional adaptation to stress and abrasion may be inferred from their morphology (Hartman, 1988; Janis and Fortelius, 1988). For instance, cusps involved in both phases of the chewing cycle, i.e., supporting cusps, have been suggested to be proportionally larger than guiding cusps, with a wider buccolingual base, less inclined occlusal surface, and thicker enamel (Khera et al., 1990). However, subtle changes in human maxillary molar morphology from anterior to posterior (Macho and Moggi Cecchi, 1992a,b; Macho and Berner, 1993, 1994; Macho, 1994) suggest functional differences between molars (Macho and Berner, 1994; Spears and Macho, 1995). Systematic changes in cross-sectional geometry, in particular, imply differences in load dissipation between first, second, and third molars (Spears and Macho, 1995). It seems possible that these differences may accord with structural modifications of the orofacial skeleton from anterior to posterior. Notably, axial inclination of molars is more pronounced posteriorly than it is anteriorly, especially with regard to mandibular molars (Dempster et al., 1963), whereas the arrangement of muscles in relation to the dental arcades may result in bite force to increase toward the posterior of the mouth (see, e.g., Mansour and Reynik, 1975a,b; Prium et al., 1978; Koolstra et al., 1988). Furthermore, the range of movements that are possible by the mandible and, hence, the angle at which teeth come into occlusion decrease progressively farther posteriorly due to the position of the temporomandibular joint (TMJ), which acts as a fulcrum for the mandible. These anatomical arrangements account for the complex functioning of the masticatory apparatus, but they may also explain, or account for, differences in molar morphology and, possibly, function. To ascertain whether both the orofacial skeleton and tooth morphology have undergone directional evolutionary change in order to ensure masticatory effectiveness, however, it is essential to gain insights into the biomechanical behaviour of various molars under differently directed loads. This is the aim of the present finite-element stress analysis (FESA).

For the present purpose, modern human molars are considered particularly suitable because of the wealth of information available on the evolution, function, and anatomy of the modern human masticatory apparatus. Moreover, by modelling a wide range of differently directed, cleavage-type loads, this study aims to first determine the loads to which that particular tooth, regardless of its position within the mouth, is apparently best adapted. Once these optimally directed loadings (defined as those that result in the least tensile stress) have been established, it will be investigated whether the findings can be reconciled with what is currently understood about the architecture of the orofacial skeleton and mastication. Although the loads applied to the present models are exceptionally high and may not be encountered normally during mastication, the trends observed will aid in determining the optimal loading direction for each molar. By taking this approach, this study attempts to provide a theoretical model of molar function based on how well these teeth dissipate loads. Thus, it will provide heuristic information about the adaptations of molars as well as the (possible) correlated evolutionary responses of the form/function complex of the orofacial skeleton and teeth. Specifically, the following questions will be addressed: 1) Where does the greatest tensile stress occur in a buccolingual plane of the tooth? 2) Are there systematic differences in biomechanical behaviour between maxillary and mandibular molars? 3) Do the results of the FESA reflect changes in molar morphology from anterior to posterior? 4) What are the implications of the findings for models of mastication?

MATERIALS AND METHODS

Sixteen unworn human maxillary molars were sectioned through the mesial cusps (M^1, n = 5; M^2, n = 6; M^3, n = 5). A description of the sample and the preparation of the sections can be found in Macho and Berner (1993, 1994). With regard to mandibular molars, images of 13 thin sections through

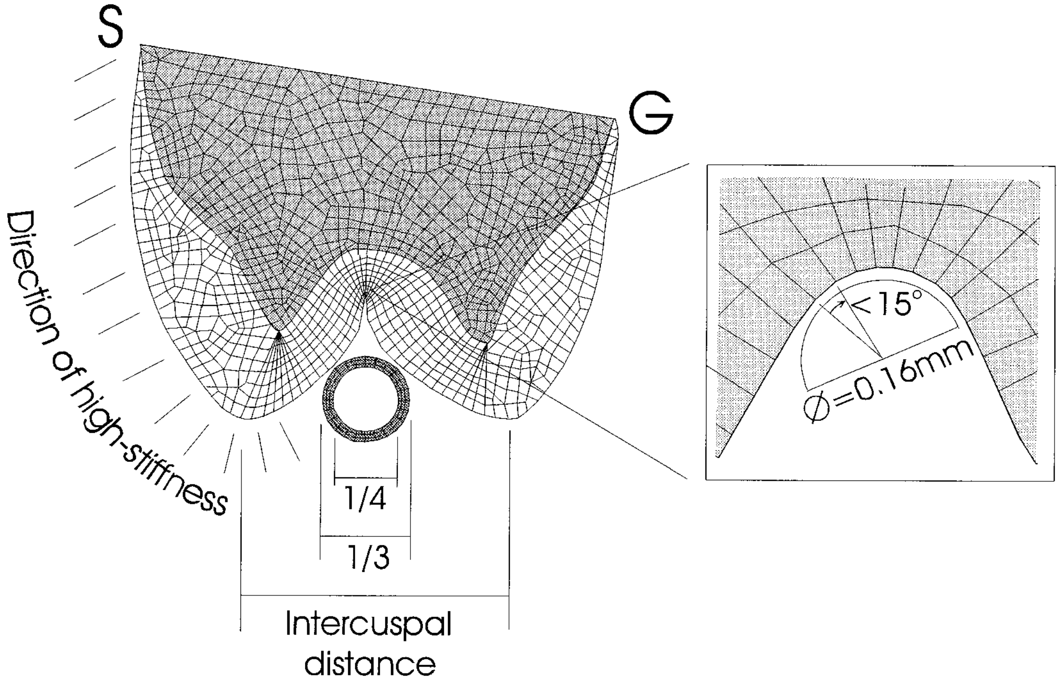

Fig. 1. Model of a maxillary second molar (M^2) showing the finite-element mesh created (S, supporting cusp; G, guiding cusp) as well as the model of the *Mezzettia* seed. The elements representing the standardised intercuspal fissure are shown.

mesial cusps (M_1, n = 5; M_2, n = 4; M_3, n = 4) were made available courtesy of David Beynon and Chris Dean. Whereas the maxillary molars were derived from a Slavic population (10th century A.D.), mandibular molars originated from recent populations of different (unspecified) ethnic origins, including San and Australian Aborigines. Thus, although sample composition is likely to increase the range of variation, it may also aid in elucidating functional adaptations that are common to modern human molars regardless of population differences. The effects of size were accounted for by scaling all teeth to the same buccolingual diameter.

The cross-sectional outline of the enamel cap was traced onto acetate paper and scanned with SAC Grafbar running under AUTOCAD (revision 12) (Autodesk, Inc.). By using AUTOCAD, the outer surface of the outline of each tooth was then digitised with 100 regularly spaced nodes, whereas the dentino-enamel junction (DEJ) was digitised with 75 nodes. The coordinates of these nodes were read into ANSYS version 5.1 (ANSYS, Inc.), the finite-element programme employed. By using node and element direct generation, a mesh of 800 plane-strain, four-noded elements was created to represent the enamel cap. Small elements were assigned in the intercuspal region to allow accurate representation of the anticipated high-stress gradient. In cases in which a fissure was present, the diameter of the pit was modelled as constant (0.16 mm), whereas the elements around the fissure were arranged so that the angle between adjacent edges did not exceed 15° (Fig. 1). The area enclosed within the DEJ and the cervical margin was meshed by using the automesh facility in ANSYS. Again, four-noded elements were specified; however, because of the irregular geometry, some three-noded elements were included (Fig. 1).

The prismatic structure of enamel was considered to behave anisotropically with respect to stiffness (Spears et al., 1993). A Young's modulus of 90 GPa was assigned to represent the along-prism properties, whereas a value of 50 GPa was used to

represent the across-prism properties of enamel. These values were predicted for enamel in which the volumetric proportion of mineralised tissue of enamel was 95% (Spears, 1997). Robinson and colleagues (1995) found that the mineral content of mature enamel ranged from less than 84% to more than 96%, whereas dental textbooks commonly give only an average of 89–91% (Boyde, 1989). Hence, although it is recognised that the values taken in this study may be relatively high, they are nonetheless within the range of mature enamel. Over- or underestimation of the true mineral content of enamel would result in an over- or underestimation of tensile stresses, respectively. However, because this study is concerned with detecting differences in load dissipation between molars rather than the prediction of fracture, the possible (systematic) effects of either over- or underestimating the actual stress values is regarded as unimportant. Prism direction is assumed to be perpendicular to the DEJ; thus, high stiffness was assigned accordingly (Fig. 1). Dentine was modelled as an isotropic material with a Young's modulus of 16.6 GPa (Waters, 1980). Poisson's ratio of both enamel and dentine was set at 0.3 (Waters, 1980).

A hollow food particle, which had an outer diameter of one-third of the respective intercusp tip distance of each tooth and an inner diameter of three-fourths of the outer diameter, was modelled (Fig. 1). ANSYS plane-strain elements with an assigned Young's modulus of 7.8 GPa were created in order to represent the properties of *Mezzettia* seeds (Lucas et al., 1991), which are known to be eaten by other primates. The properties of *Mezzettia* seeds were chosen because they are tough, strong, and stiff and, thus, will exert potentially damaging conditions to the tooth. Poisson's ratio of the seed was again set at 0.3. The food particle was then placed onto the tooth model, and tooth-food contact was modelled by using contact elements. Frictionless contact was specified.

Instead of an opposing molar pushing the food particle into the occlusal basin, a long beam with an extremely high stiffness, which ensured negligible deformation during simulation, was used. The displacement of the beam was always in the direction perpendicular to its long axis. The occlusal plane was defined as the straight line joining the cusp tips, and the lingual cusps were always kept to the left (Fig. 2). Three loads were modelled: -30°, 0°, and +30°. When the beam model was held parallel to the defined occlusal plane, a value of zero degrees was assigned. Rotation of the beam toward positive angles always resulted in loads being exerted predominantly on the guiding cusps, whereas negative angles consistently loaded the supporting cusps (Fig. 2).

Breakdown of the food particle modelled here (i.e., a two-dimensional representation of a hollow cylinder) is most likely the result of tensile stress. At the instant at which tensile stress within the food reached the ultimate tensile stress (UTS) of *Mezzettia* seed (67 MPa), the maximum value of stress within the tooth was recorded. The values of maximum tensile stress were then compared for the various teeth and for various loading angles. Statistical analyses, which helped to elucidate trends within and between teeth at comparable loads, were performed in Microsoft Excel (version 6.0; Microsoft Corporation, Redmond, WA).

RESULTS

The typical pattern of tensile stress distribution (first principal stress) in molars at the point at which stresses in the seed reach ultimate levels is shown in Figure 3 for maxillary and mandibular second molars. Maximum tensile stress in the particle always occurred along the inner surface directly below the point of beam-food contact. With regard to the tooth, maximum tensile stress in the enamel always occurred in and around the intercuspal fissure.

With regard to maxillary molars, the stresses in M^1s ranged from 4.97 MPa (+30°) to 6.93 MPa (0°), but differences between differently directed loads were not statistically significant by analysis of variance (ANOVA; Table 1). In contrast, highly significant differences were found in M^2s, whereby loads exerted toward the guiding cusp (+30°) gave significantly lower values (4.28 MPa) than those directed toward the supporting cusp (-30°; 10.17 MPa) or both (10.35 Mpa) (Table 1). A similar but less marked trend was found for M^3 molars: Again, the lowest

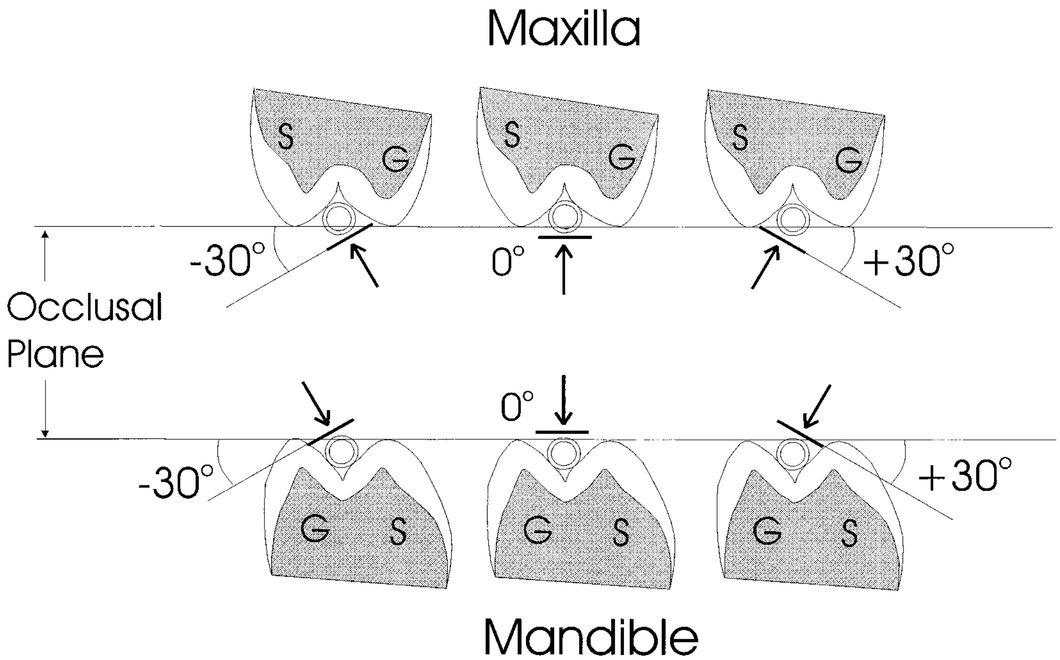

Fig. 2. The occlusal plane is the straight line joining the cusp tips. The angles at which the food particle was loaded by the beam are shown for maxillary and mandibular molars.

tensile stresses were yielded when loads were exerted on guiding cusps (3.71 MPa; Table 1). Overall, although guiding cusps of maxillary molars appeared to be better at dissipating loads throughout the series, this was more marked posteriorly than anteriorly: first maxillary molars are more uniform in their biomechanical behaviour (Table 1, Fig. 4). Conversely, in mandibular molars, supporting cusps were consistently better at dissipating loads regardless of tooth position (Table 2): these trends became statistically significant posteriorly (Table 2). Hence, although differently directed loads produced statistically significant results in both maxillary and mandibular molars, these trends were dissimilar for upper and lower molars and apparently were not complementary (Fig. 4). Along each tooth row, tensile stresses between teeth at a particular angle of load were never statistically significant (Tables 1, 2; Fig. 4).

To ascertain the strength of the observed trends, the difference in resulting tensile stress between supporting and guiding cusp loading was calculated, and paired t-tests were employed (Table 3). In maxillary molars, statistically significant t values were only obtained for M^2s and for the combined sample, whereas, in mandibular molars, all paired t-tests provided statistically significant results (Table 3). Figure 5 graphically depicts and explains these findings. Although there is a general tendency for maxillary guiding cusps to dissipate loads more effectively than functional cusps, a number of teeth did not follow such a clear-cut pattern, which may have resulted in the high standard deviations and nonsignificant t-test results shown in Table 3. All mandibular molars, on the other hand, consistently performed best when the supporting cusp was loaded (Fig. 5), thus exhibiting a clear directionality in load dissipation between buccal and lingual cusps.

Finally, Student's t-tests between maxillary and mandibular molars were performed for all angles of loadings separately (Table 4). There was no statistically significant difference between maxillary and mandibular M^1s, as expected (Tables 1, 2; Fig. 4); however, in M^2s, loads directed toward the

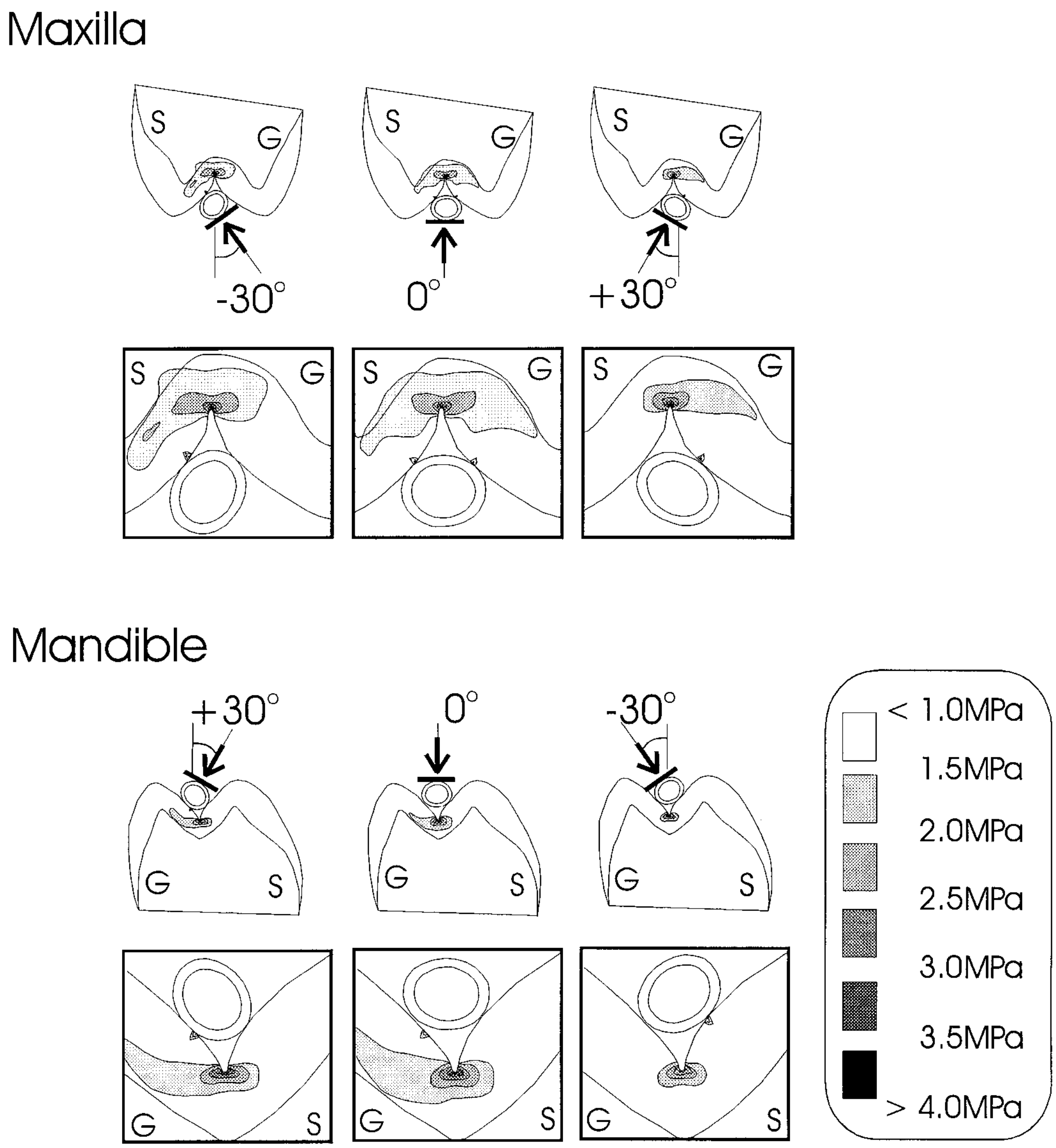

Fig. 3. Contour maps of the distribution of first principal stresses at the intercuspal region for various angles of beam displacement are shown for a maxillary second molar and a mandibular second molar.

supporting cusps were statistically significantly better dissipated in mandibular molars than in maxillary molars ($P < 0.01$), whereas loads exerted at the guiding cusps of maxillary molars were better dissipated than the equivalent loads oriented at mandibular molars ($P < 0.05$). Similar trends were observed for third molars, although the results were statistically significant only for guiding cusps ($P < 0.05$). Along the tooth row, maxillary molars consistently yielded lower average maximum stresses than mandibular molars when the guiding cusps were loaded (Table 4, Fig. 4).

DISCUSSION

Although few would dispute that differences exist between maxillary and mandibu-

TABLE 1. Descriptive statistics of maximum principal stress (MPA) found in maxillary molars when loads are applied at different angles[1]

		−30° (supporting cusp)		0°		+30° (guiding cusp)		ANOVA	
Molar	No.	Mean	SD	Mean	SD	Mean	SD	*F* value	*P*
M^1	5	5.27	1.37	6.93	2.60	4.97	1.97	1.34	0.298
M^2	6	10.17	3.40	10.35	3.61	4.28	1.38	8.11	0.004*
M^3	5	7.25	4.76	7.78	4.00	3.71	0.95	1.86	0.198
F value		2.81		1.48		0.90			
P		0.097		0.264		0.431			

[1] Results of analysis of variance (ANOVA) are also given between different angles of loading as well as for differences between teeth at the same loading.
* $P < 0.01$.

lar molars or between molars along the tooth row, the biomechanical behaviour of these teeth remains unclear and cannot be determined from inspection of morphology alone. FESA affords the opportunity to predict the stresses in biological structures, especially in those that are not amenable to direct mechanical experiments (for example, through strain gauges), such as teeth (Yettram et al., 1976; Rubin et al., 1983; Khera et al., 1988; Goel et al., 1990, 1991, 1992). Hence, FESA was employed here to assess the effects of cleavage-type loads on molars. These loads, which cause outward displacement of cusps implicated in the origins of cuspal fractures (Granath and Svensson, 1991; Panitvisai and Messer, 1995), are particularly useful for the present purposes, because loads exerted to the occlusal basin, i.e., below the cusp tips, are likely to yield similar stress distributions within the tooth regardless of whether it is unworn or slightly worn. Moreover, although it is recognised that the loads employed here are unlikely to occur during normal mastication (i.e., modern humans do not eat anything as tough and strong as *Mezzettia* seeds), they are likely to shed light on the optimal loading directions.

Given the wide range of loading regimes to which molars are exposed during life, i.e., through differential wear (Osborn and Lumsden, 1978) and foods consumed (Wang and Stohler, 1991), it is not assumed here that teeth are designed optimally toward one particular loading condition (Pfretzschner, 1995). Nonetheless, it is anticipated that tooth morphology will limit the range of differently oriented loads that it can resist to those directions that are encountered most frequently during normal mastication. It is the aim of the present study to determine these limits and to enquire whether these restrictions in acceptable stress distributions can be related to the form/function complex of the orofacial complex as a whole. In other words, does the biomechanical behaviour of isolated teeth provide information about the masticatory apparatus?

Limitations

Because chewing involves predominantly vertical and mediolateral movements of the mandible, it is reasonable to assume that most of the forces exerted on the tooth will occur in a buccolingual plane. Hence, although the advantages of three-dimensional finite-element models are recognised, two-dimensional models are considered to be sufficient to determine the mechanical adaptations of isolated molars within the orofacial skeleton.

Enamel is particularly weak under tension (Bowen and Rodriguez, 1962; Lee and Eakle, 1984, 1996), and the strength of the tooth under a given load, thus, will depend largely on its ability to minimise tensile stresses. In all instances, tensile stresses tended to concentrate in the intercuspal fissure, which is unsurprising in light of the fact that, in general, sharp corners concentrate stress. There are, however, a number of other factors that may have affected the results.

Human enamel is predominantly prismatic (Meckel et al., 1965), and, due to differences in crystal orientation within prisms and the interprismatic matrix,

enamel is stiffer along the direction of prisms than across them (Spears, 1997). In the present FESA models, prisms were assumed to be perpendicular to the DEJ (Fig. 1). Although this is largely correct, however, it should be borne in mind that prisms do not grow straight from the DEJ to the outer enamel surface but take a more or less wavy course (Kawai, 1955), whereas prism arrangements are even more complex in cuspal (and intercuspal) regions (Hirota, 1982; Osborn, 1968). Evolutionary responses of enamel microstructure to counteract potentially damaging tensile stresses are well documented (see, e.g., Rensberger and Pfretzschner, 1992), although information about the microstructure in the intercuspal regions is not available. Thus, the simple model of radiating enamel prisms employed here is likely to have affected the magnitude or damage potential of the predicted stresses, which could have been further compounded by possible (systematic?) differences in chemical composition of mature enamel within and between teeth (Robinson et al., 1995). Also, the fact that the diameter of the intercuspal fissure was standardised for the present models and the fact that the possibility of surface flaws was ignored may have influenced the results. Overall, it follows that stresses or their damaging effects on teeth may be lower than predicted here. Interpretation of results will therefore focus predominantly on relative changes in load dissipation within and between molars.

The decision to pay more attention to proportional changes rather than absolute values seems further warranted by the fact that the properties assigned to the food particle modelled are those of a *Mezzettia* seed. Although it is eaten by other hominoids, this seed is too tough and strong for human consumption; thus, stress values are unrealistically high. Given the fact that all materials are modelled as linear elastic, it should be noted that a reduction of the stiffness and strength of the food particle would reduce, but not eliminate, the tensile

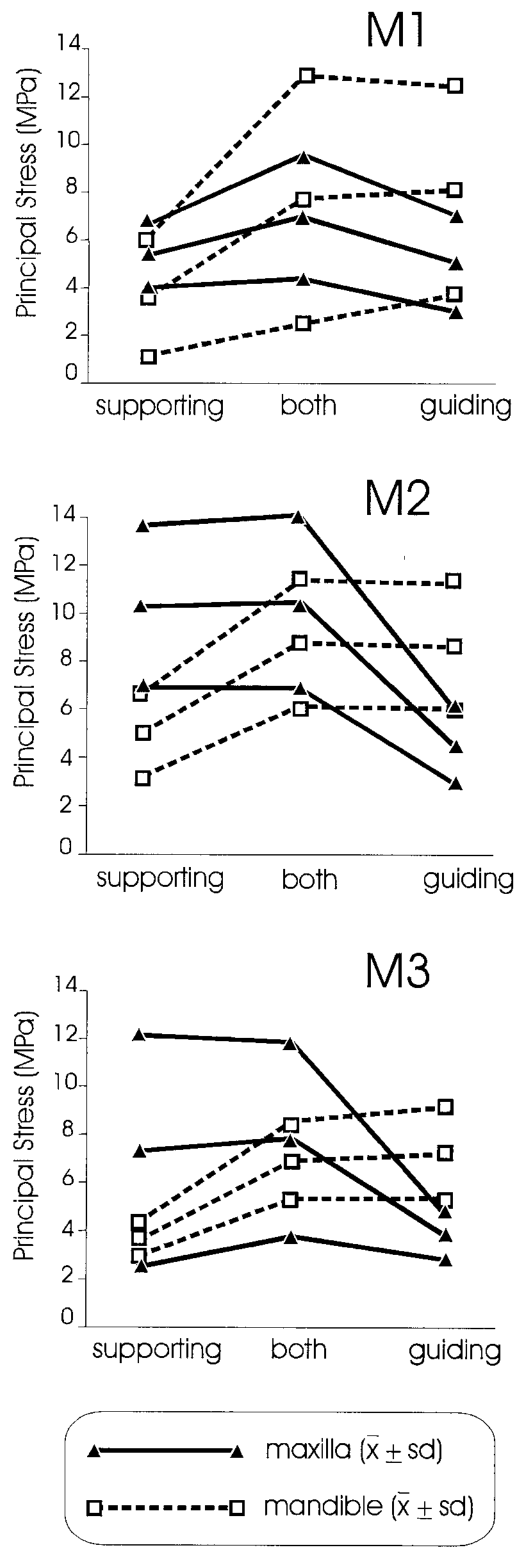

Fig. 4. Mean values and standard deviations of principal tensile stresses for each angle of loading are shown by tooth category.

TABLE 2. Descriptive statistics of maximum principal stress (MPA) found in mandibular molars when loads are applied at different angles[1]

		−30° (supporting cusp)		0°		+30° (guiding cusp)		ANOVA	
Molar	No.	Mean	SD	Mean	SD	Mean	SD	*F* value	*P*
M_1	5	3.56	2.46	7.64	5.14	8.04	4.35	1.79	0.209
M_2	4	4.85	1.66	8.64	2.62	8.56	2.57	3.47	0.076
M_3	4	3.52	0.69	6.86	1.56	7.19	1.89	7.61	0.012*
F value		0.70		0.23		0.18			
P		0.519		0.792		0.838			

[1] Results of analysis of variance (ANOVA) are also given between different angles of loading as well as for differences between teeth at the same loading.
* $P < 0.05$.

TABLE 3. Differences in maximum stress between cleavage-type loads exerted on the supporting cusp (−30°) and guiding cusp (+30°)[1]

	Supporting-guiding cusp			Paired t-test	
Molar	No.	Mean	SD	t value	*P*
Maxilla					
M^1	5	0.30	2.16	0.31	0.770
M^2	6	5.90	3.83	3.77	0.013*
M^3	5	3.54	4.15	1.90	0.129
Total	16	3.41	4.05	3.37	0.004**
Mandible					
M_1	5	−4.48	3.25	−3.08	0.037*
M_2	4	−3.71	2.26	−3.27	0.047*
M_3	4	−3.67	1.72	−4.26	0.024*
Total	13	−3.99	2.39	−6.03	0.000***

[1] Results of paired t-tests are also shown.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

stress present in the intercuspal fissure. Because chewing is a cyclical process, these tensile stresses, although relatively low, occur on a repetitive basis. Such stresses may induce fatigue failure even at levels far below those reported for the ultimate tensile strength of enamel. Although it is possible that there is a physical limit below which tensile stresses cannot traumatise the tooth, such consistently low levels are unlikely to be maintained during normal mastication (i.e., puncture crushing and chewing) given the range of foods habitually consumed by modern humans. Thus, during evolution, durability of molars may have been maximised by strengthening those cusps that undergo (or have undergone) greater loads with regard to both magnitude and frequency: these cusps would be expected to minimise tensile stress most effectively. This study aims to explore trends in load dissipation among human molars with respect to considerations that the patterns and magnitudes of tensile stresses may shed light on the biomechanical adaptation of molars. No attempts will be made to determine accurately when these teeth are likely to break.

Stress distribution in molars

The masticatory apparatus forms a highly integrated system. Although it displays a great amount of bilateral symmetry, shifts in morphology and function occur mainly in the anteroposterior direction. Hence, intercuspating molars, which have been likened to forming a "mortar-and-pestle" system (Kay and Hiiemäe, 1974; Lucas, 1979), such that the occlusal basins of both upper and lower molars would resemble mortars, whereas the supporting cusps may act as pestles, would be expected to change in concert from anterior to posterior.

Although first maxillary molars appear to be well designed to resist loads directed toward the occlusal basin at different angles, tensile stresses in mandibular first molars are proportionally lower when loads are exerted toward the supporting cusps. This effectiveness of mandibular buccal cusps is retained along the tooth row, but tensile stresses induced by loads directed away from the supporting cusp increase from anterior to posterior (Figs. 4, 5; Tables 1–4). Conversely, M^2s and M^3s are well adapted to resist loads exerted predominantly on the guiding cusps. Thus, maxillary and mandibular molars exhibit dissimilar anteroposterior changes, which casts doubt on the presumed integrated nature of the masticatory apparatus.

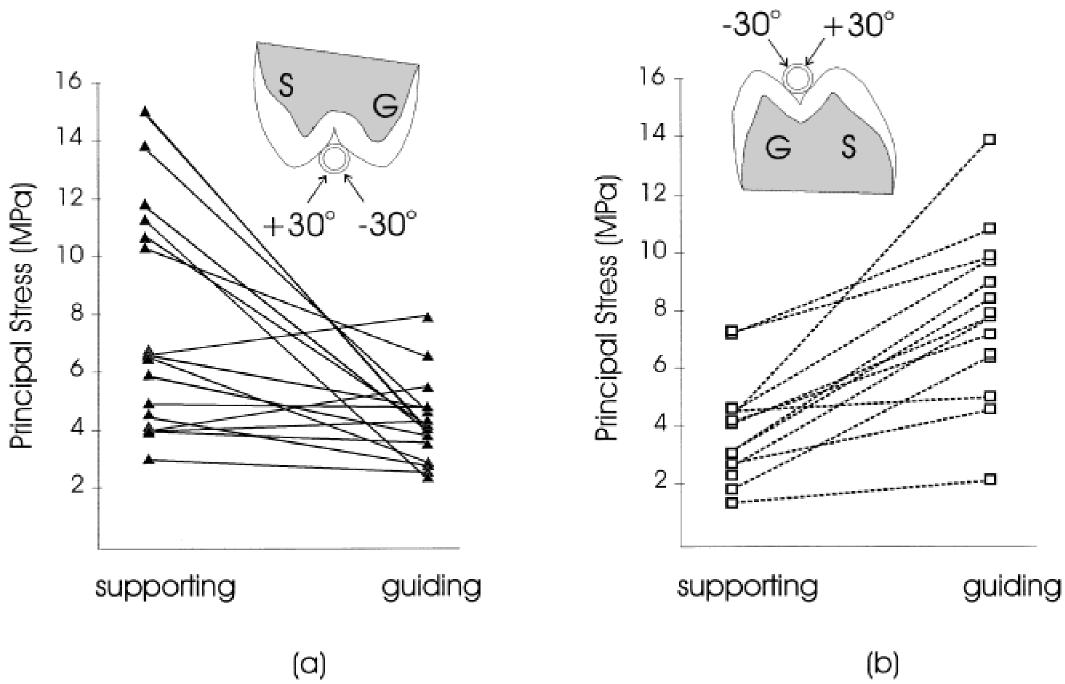

Fig. 5. The difference in principal tensile stress between supporting (+30°) and guiding (-30°) cusp loading is plotted separately for each maxillary (**a**) and mandibular (**b**) molars.

TABLE 4. Student's t-tests between maximum stresses in maxillary and mandibular molars at different angles of loading

	−30° (supporting cusps)		0°		+30° (guiding cusps)	
Molars	t value	*P*	t value	*P*	t value	*P*
M1	1.36	0.223	−0.27	0.793	−1.44	0.221
M2	3.30	0.011*	0.87	0.410	−3.04	0.038*
M3	1.73	0.158	0.47	0.660	−3.35	0.028*

* $P < 0.05$.

During human evolution, advancements of food preparation techniques since the Mesolithic period have reputedly led to a relaxation of selection pressures on teeth, thus resulting in molars undergoing evolutionary changes that were not accompanied (invoked?) by the functional restructuring of the orofacial skeleton (see, e.g., Brace et al., 1987, 1991). If this is the case, however, then molars would be expected to vary randomly. Given the present sample composition, the systematic directional changes in stress distribution within and between molars are therefore even more surprising (Table 3, Fig. 4) and clearly refute propositions that random mutations affecting tooth size and morphology have accumulated during evolution. Rather, it would seem that each modern human molar category is suited to resist a certain range of loads irrespective of ethnic origin.

In (ideal) occlusion, the supporting cusps of mandibular molars are expected to push the bolus against the occlusal basin of maxillary molars, whereas maxillary lingual cusps would concomitantly push it against the occlusal basin of lower molars. Stress patterns induced by differently directed cleavage-type loads do not support this simplistic mortar-and-pestle model of mastication. Although the consistent results obtained for supporting cusps of mandibular molars could imply that they play the role of pestles, findings for maxillary molars are inconclusive: The results neither suggest that one particular cusp may be well designed to act as a pestle, nor do they indicate unequivocally that maxillary molars might perhaps provide the basin against which food is crushed/ground. The behaviour of molars in

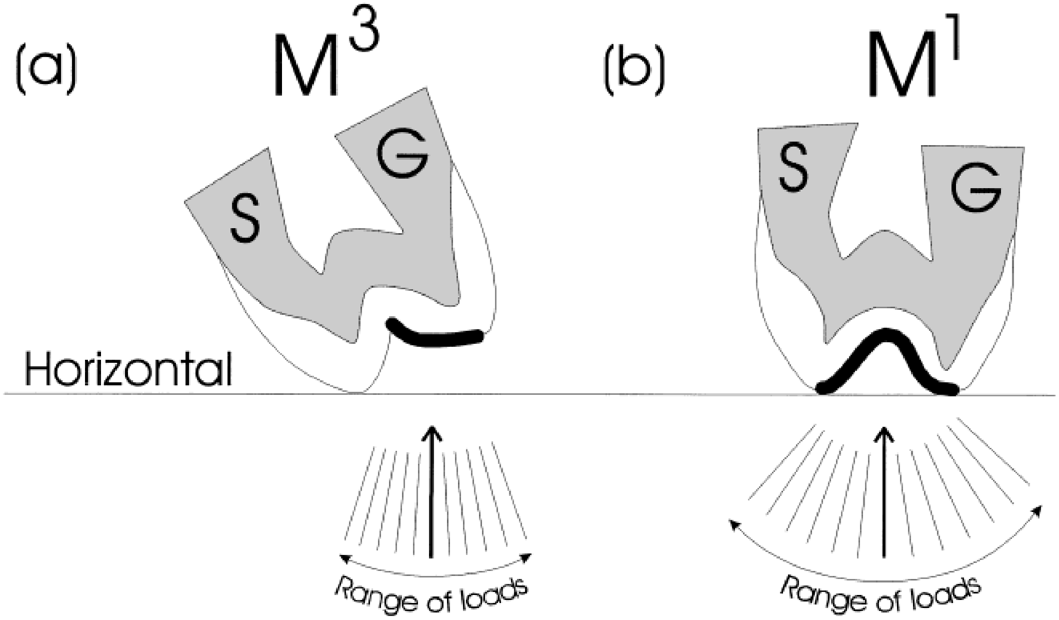

Fig. 6. Illustration indicating the surface at which the molar can effectively resist loads. Near-vertical loads are well dissipated in coronally inclined third maxillary molars (**a**), whereas noninclined first maxillary molars are able to resist differently directed loads (**b**).

mastication, thus, may be more complex than was thought previously.

Molars in mastication

In modern humans, the inclination of molars increases progressively from anterior to posterior both in the sagittal and the coronal plane (Dempster et al., 1963; Smith, 1986). Although much emphasis has been placed on the biomechanical implications of axial inclination of molars in the sagittal plane (Baragar and Osborn, 1987; Osborn, 1993), coronal inclination of molars has been implicated mainly in the development of a helicoidal pattern of wear (Osborn, 1982; Richards and Brown, 1986; Smith, 1986). However, patterning of enamel thickness distribution within and between maxillary molars suggests that posterior molars are adapted to function differently from anterior molars (Macho and Berner, 1994). This suggestion seems to be supported further by the present findings. Due to their increased inclination, the occlusal surfaces of the guiding cusps of maxillary posterior molars become oriented more horizontally, whereas those of the supporting cusps face vertically (Fig. 6a). Hence, near-vertical loads on posterior molars, by necessity, would be exerted predominantly on guiding cusps (Fig. 6a). Less inclined anterior molars should be adapted to resist loads that are exerted more directly toward the occlusal basin (Fig. 6b). Moreover, due to

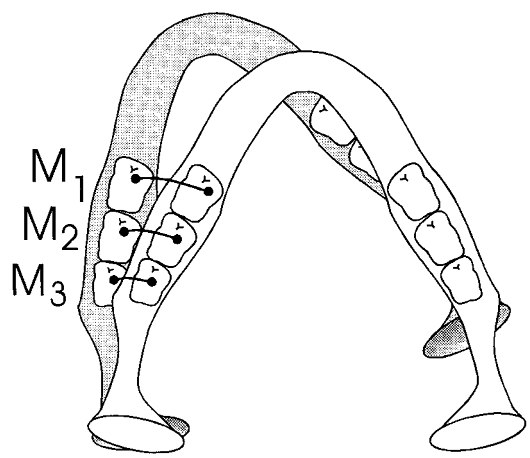

Fig. 7. Lateral movement of the mandible showing the decrease of lateral excursion possible from first to third molars.

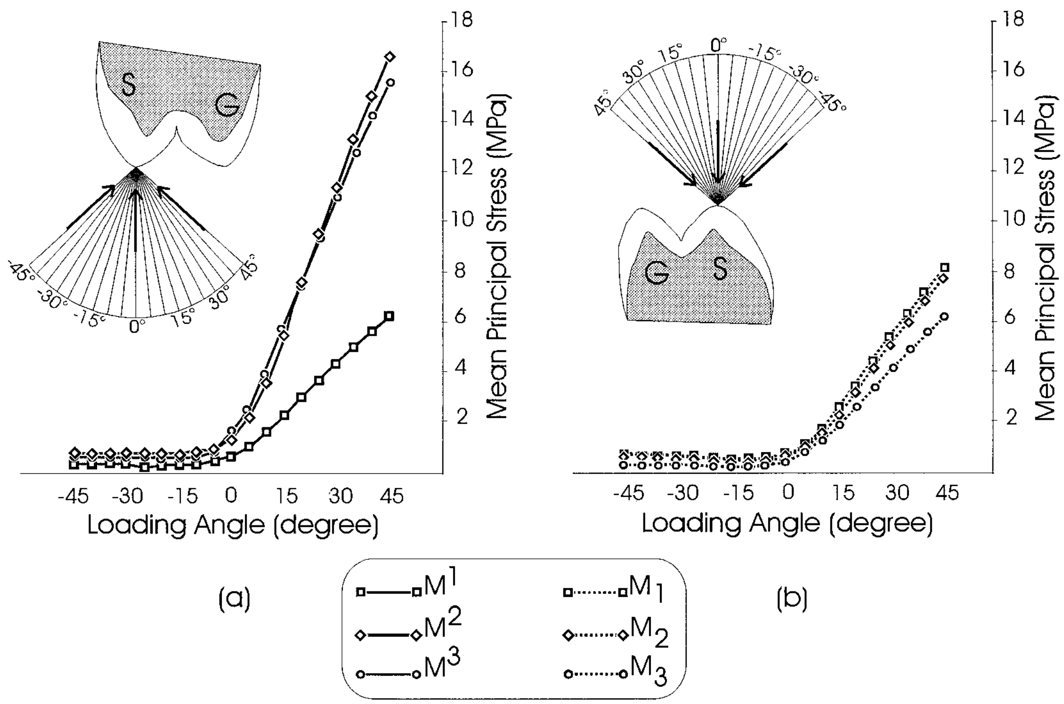

Fig. 8. Mean values of maximum principal tensile stresses at the intercuspal fissure resulting from differently directed loads at the supporting cusps of maxillary (**a**) and mandibular (**b**) molars.

the greater lateral excursion that is possible by the mandible farther anteriorly, first maxillary molars must resist a wider range of differently directed loads than posterior molars (Fig. 7). In other words, the likelihood of food being pushed against maxillary molars at different angles is greater anteriorly than posteriorly. Conversely, inclined posterior maxillary molars are apparently well adapted to resist near-vertical loads on guiding cusps, and, because bite-force is maximised in posterior molars (see, e.g., Mansour and Reynik, 1975a,b; Pruim et al., 1978; Koolstra et al., 1988) and is created most efficiently when it is directed near vertically and parallel to the direction of the main masticatory muscles (Baragar and Osborn, 1987; Osborn, 1993), they probably have to. Hence, with regard to maxillary molars, tooth design appears to complement the architecture of the orofacial skeleton.

This model of mastication, however, assumes that maxillary molars are likely to provide the mortar against which the bolus is crushed/ground, whereas mandibular molars act as “pestles.” Although this is implicated by the results of the cleavage-type loads, it has not been substantiated. Moreover, anteroposterior modifications of the orofacial skeleton appear to have had little effect on the patterns of stress distribution within mandibular molars. This raises questions of whether the present findings can be reconciled with the model of mastication outlined above.

To gain further insights into the possibility of supporting cusps of mandibular molars behaving like pestles, differently directed point loads at 3.5 KN were applied to the cusp tips of supporting cusps of maxillary and mandibular molars, respectively (Fig. 8). These forces correspond to those necessary to induce failure in the food particle using cleavage-type loads (i.e., 3.2–3.7 KN). Although they are unrealistically high and are confounded by the fact that cusp tips are worn rapidly, these loads, nonetheless, may complement the results obtained from occlusal basin loads.

Overall, tensile stresses at the intercuspal regions are lower in mandibular molars

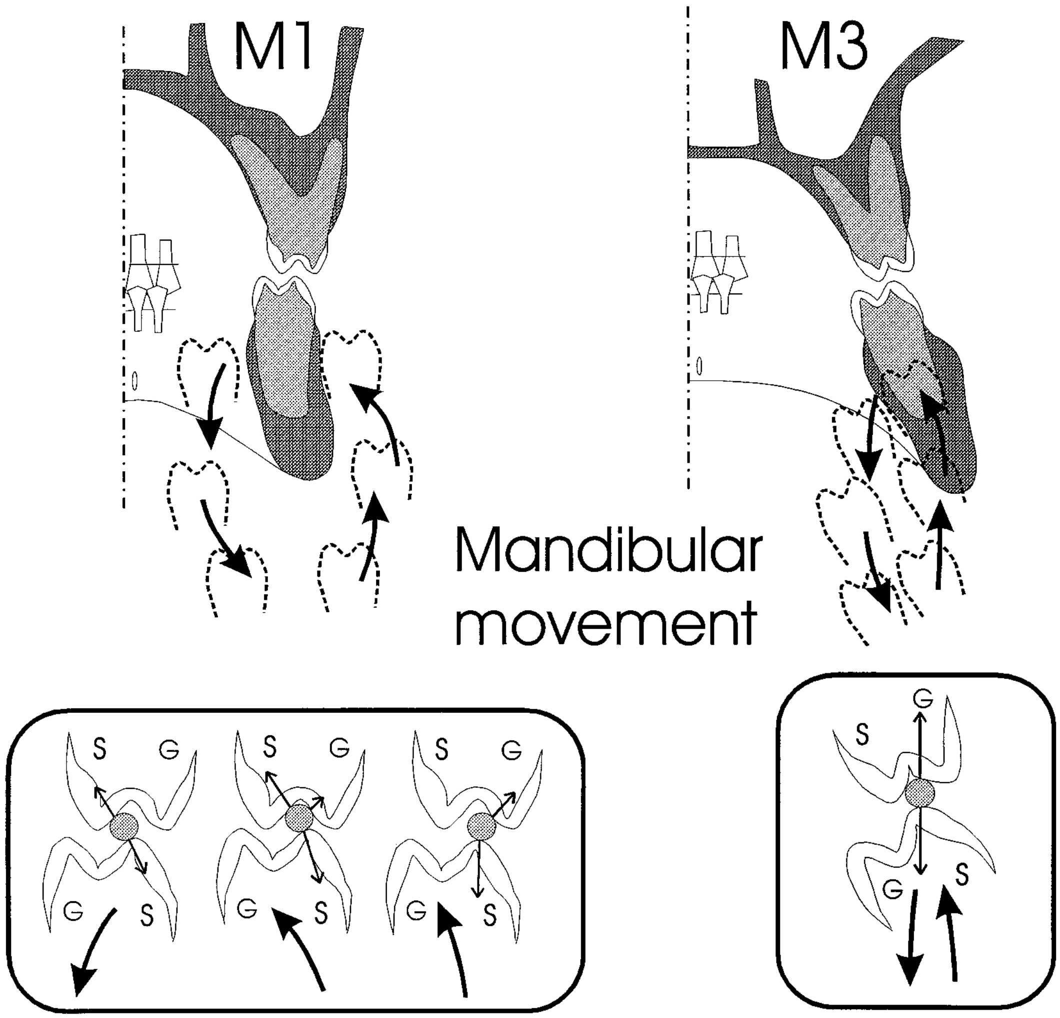

Fig. 9. Loads expected to be exerted on different molars during mastication based on the structure of the orofacial skeleton and the patterns of stress distribution within and between molars by using finite-element stress analysis.

than in maxillary molars. Although lingual cusps of first maxillary molars resist differently oriented loads well, in accordance with their ability to act as pestles, values obtained for second and third maxillary molars are dangerously high (Fig. 8). This is not the case for mandibular molars, which give consistently low values; in fact, overall tensile stresses tend to decrease from anterior to posterior. It is of note that, when they are loaded at negative angles, i.e., from the outside of the cusp tip toward the occlusal basin, tensile stresses remain negligible.

Although it is well documented that the overall crush/shear ratio increases posteriorly in primates, it is particularly noteworthy here that the mean pit diameter on the buccal side of mandibular supporting cusps apparently increases from M_1 to M_3, at least in chimpanzees (Gordon, 1982). Although the larger pits on third molars indicate greater compressive forces on these posterior teeth, the position of the wear facets on the buccal side of the cusps as well as their clear definition of microwear features support suggestions that these cusps not only

act as pestles but, due to their greater coronal inclination, sustain inwardly directed loads on the supporting cusps (Fig. 9). Such changes in microwear features may be even more marked in *Homo*, in which a greater degree of axial inclination is exhibited than in *Pan* (Smith, 1986). In the present study, cleavage-type and cuspal point loads both indicate that buccal cusps of mandibular molars are strong, regardless of tooth position, and probably act as pestles, whereas maxillary molars are more likely to provide "mortars" (Fig. 9). Although this is not to deny that protocones of posterior maxillary molars are likely to occlude with the talonid basin of mandibular molars during chewing, the findings suggest that posterior buccal cusps may assume greater importance during puncture crushing. Detailed microwear analyses have a high resolution (Teaford, 1994), and documentation of anteroposterior changes in maxillary and mandibular microwear patterns, for example, could help resolve this proposition. Indirect support, however, is provided by tooth morphology and clinical evidence, as outlined below.

Maxillary molars, in accordance with their role in providing the mortar, have generally more divergent tooth roots than mandibular molars, especially anteriorly (Aiello and Dean, 1990), whereas maxillary molars have overall thicker enamel (Martin, 1983). The coronal tilt of maxillary molars makes it necessary that guiding cusps are capable of resisting loads that are exerted during puncture crushing and the closing/power stroke; however, due to their greater coronal inclination (Dempster et al., 1963), buccal cusps of mandibular molars are rendered more pronounced than lingual cusps, thus making them more suitable to act as pestles. If this model of molar (cusp) specialisation and intercuspation is correct, then it may also explain the relatively high incidence of cuspal fractures of mandibular guiding cusps (Cavel et al., 1985; Eakle et al., 1986) when they are brought into occlusion accidentally: Maxillary guiding cusps do not seem to be particularly susceptible to fractures.

Taken together, a model of mastication can thus be proposed in which it is not the mortar that ". . . is moved across the pestle. . ." (Kay and Hiiemäe, 1974, p. 231). Rather, it appears that supporting cusps of mandibular molars are moved across the mortar, which, however, becomes increasingly restricted in its expansion posteriorly due to modifications of the orofacial skeleton as a whole (Fig. 9).

SUMMARY AND CONCLUSIONS

"Since the masticatory apparatus functions as an integrated unit, it follows that the structure of any of its parts can only be explained in terms of its function and that with reference to the mechanism of function of the system as a whole" Hiiemäe (1967, p. 885).

In describing the typical chewing cycle, the maxilla, despite its contribution to masticatory movement by flexion and extension of the cranium, is regarded conventionally as fixed, whereas the movements of the mandible are described in relation to this fixed plane (Griffin and Malor, 1974; Hiiemäe and Kay, 1972; Hiiemäe, 1978). Mandibular molars are brought into centric occlusion at different angles, depending on the properties of foods consumed (see, e.g., Wang and Stohler, 1991) and whether food is being puncture crushed or chewed. Although comminution of food is a cyclical process, there are nonetheless marked differences between puncture crushing and chewing (Hiiemäe and Kay, 1972), whereby the former is characterised by predominantly vertical movements and tooth-food-tooth contact, whereas the latter involves a greater mediolateral component and occasional tooth-tooth contact. Because of the position of the TMJ in relation to the dental arcade as well as the arrangement of muscles of mastication, puncture crushing is likely and most effectively performed posteriorly (van Eijden, 1991), whereas chewing can take place effectively farther anterior at a lesser force. The orofacial morphology, the arrangement of muscles of mastication, and the biomechanical behaviour of teeth indicate that this is the case. Thus, the present FESA results further highlight the integrated nature of tooth morphology and the orofacial skeleton. Moreover, to ensure the effectiveness of the masticatory apparatus, maxillary and mandibular molars have apparently become specialised during evolution, whereby the former

provide the basin against which the food is crushed/ground, whereas the latter may act as a pestle. However, the area of maxillary molars over which the food can be processed effectively becomes increasingly restricted from anterior to posterior, probably as a result of anteroposterior changes observed in the architecture of orofacial skeleton. Of all molars studied, M^1s seem to be most versatile and the most well suited to dissipate loads directed at them from different angles; they may act as either mortars or pestles.

Although this study has focused on modern human molars only, because sufficient information is available on the anatomy and function of the human masticatory apparatus, the present findings are likely to have implications for palaeontological and clinical studies. Despite reputed relaxation of selection pressures on modern human teeth since the Mesolithic period, systematic and statistically significant differences were found between molars. Molars are adapted to different loading regimes in accordance with the functioning of the masticatory apparatus. In light of the observed trends, it is reasonable to suggest that other mammals may have undergone similar directional modifications of both teeth and the orofacial skeleton in order to facilitate effective breakdown of food (Macho and Spears, submitted). Hence, functional inferences based on isolated teeth without due regard of the orofacial skeleton may not be justified and are likely to be misleading.

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